

Reviews, Critiques and New Ideas

Taxonomy and phylogeny of the genus *Mycosphaerella* and its anamorphs

Crous, P.W.

CBS-KNAW Fungal Biodiversity Centre, Uppsalalaan 8, 3584 CT Utrecht, The Netherlands

Crous, P.W. (2009). Taxonomy and phylogeny of the genus *Mycosphaerella* and its anamorphs. *Fungal Diversity* 38: 1–24.

Historically plant pathogenic species of *Mycosphaerella* have been regarded as host-specific, though this hypothesis has proven difficult to test largely due to the inavailability of fungal cultures. During the course of the past 20 years a concerted effort has been made to collect these fungi, and devise methods to cultivate them. Based on subsequent DNA sequence analyses the majority of these species were revealed to be host-specific, though some were not, suggesting that no general rule can be applied. Furthermore, analysis of recent molecular data revealed *Mycosphaerella* to be poly- and paraphyletic. Teleomorph morphology was shown to be too narrowly defined in some cases, and again too widely in others. *Mycosphaerella* and *Teratosphaeria* as presently circumscribed represent numerous different genera, many of which can be recognised based on the morphology of their 30 odd associated anamorph genera. Although *Mycosphaerella* is generally accepted to represent one of the largest genera of ascomycetous fungi, these data suggest that this is incorrect, and that *Mycosphaerella* should be restricted to taxa linked to *Ramularia* anamorphs. Furthermore, other anamorph form genera with *Mycosphaerella*-like teleomorphs appear to represent genera in their own right.

Key words: Anamorphs, *Capnodiales*, *Mycosphaerella*, polyphyletic, *Teratosphaeria*, systematics

Article Information

Received 9 June 2009

Accepted 6 July 2009

Published online 1 October 2009

*Corresponding author: Crous, P.W.; e-mail: p.crous@cbs.knaw.nl.

Introduction

Species of *Mycosphaerella* have adapted in various ways to different ecosystems, and vary from being saprobic, plant pathogenic to hyperparasitic (de Hoog *et al.*, 1991; Goodwin *et al.*, 2001; Jackson *et al.*, 2004; Arzanlou *et al.*, 2007b). *Mycosphaerella* spp. are among the most common and destructive plant pathogens known, causing considerable economic losses on a wide variety of host plants worldwide, including economically important crops such as banana, cereals, sugar beet, strawberry, soybean, citrus, eucalypts, acacia, pines and many others (Farr *et al.*, 1995; Crous and Braun, 2003). Plant pathogenic *Mycosphaerella* species are mainly follicolous,

although some are associated with stem cankers (Cortinas *et al.*, 2006), fruit lesions (Pretorius *et al.*, 2003) or blemishes, spots and specks (Batzer *et al.*, 2008). Damage is usually due to defoliation, which reduces the photosynthetic capacity of the crop, leading to growth loss. Some species, such as *M. citri*, affect both leaves and fruits. Others such as *M. fijiensis*, infect banana leaves, thereby reducing the photosynthetic capacity of the crop, and also induce physiological changes resulting in premature ripening of fruit (Carlier *et al.*, 2000; Marin *et al.*, 2003).

The first generic description for *Mycosphaerella* (1884) was that of *Sphaerella* (1882). Saccardo placed all species of *Sphaeria* with presumably 1-septate, hyaline ascospores

in *Sphaerella*. The genus *Sphaerella* was, however, already in use for green algae, and thus all these taxa had to be placed in *Mycosphaerella* (Aptroot, 2006), which is based on *M. punctiformis* (Verkley *et al.*, 2004). Despite the hyaline, 1-septate ascospores reported in the type by Persoon (1794), most authors at the beginning of the 19th century worked without microscopes, and thus what they described as a *Sphaeria* or *Sphaerella* species, literally meant a ‘spherical’ fruiting body (Aptroot, 2006). Soon it became standard to also describe collections from different hosts as new species, which later led to many taxa being reduced to synonymy (Von Arx, 1949; Barr, 1972; Tomilin, 1979; Corlett, 1991; Aptroot, 2006). In the recent revision of *Mycosphaerella* names, Aptroot (2006) treated close to 10,000 taxa, recognising around 3,000 species.

In her treatment of North American taxa, Barr (1972) recognised two subgenera, *Eu-Mycosphaerella* and *Didymellina* (including the section *Cymadothea*), and 10 sections. The sub-genera were separated on the basis of the shape of their asci and anamorphs, and the sections based on ascospore shape, and/or parasitic or saprobic habit. Von Arx (1983) found the subdivision unsatisfactory, because the characters were inordinately divergent.

The sections of Barr were refined by Crous *et al.* (2000) as follows

Section *Mycosphaerella*: cylindrical asci and mostly uniseriate, thin-walled, often small ascospores that are constricted at the septum and inequilateral, with rounded upper ends. Anamorphs: typically *Ramularia* with *Asteromella* spermatial states. Representative species: the common polyphagous *M. punctiformis*.

Section *Tassiana*: pyriform asci and irregularly arranged, thick-walled ascospores that are often large and constricted at the septum and nearly equilateral, relatively broad with rounded ends, containing irregular lumina. Anamorph: *Cladosporium s. str.* Representative species: the common polyphagous species *Davidiella tassiana*. Further research supported the decision of David (1997) to place *Heteroconium* anamorphs in *Cladosporium*, while section *Tassiana* was elevated to generic level as *Davidiella* (*Cladosporium* anamorphs)

(Braun *et al.*, 2003; Crous *et al.*, 2007a; Schubert *et al.*, 2007a,b; Zalar *et al.*, 2007), for which the family *Davidiellaceae* was established (Schoch *et al.*, 2006).

Section *Caterva*: cylindrical asci and irregularly arranged, thin-walled, often medium-sized ascospores, that are rarely constricted at the septum and inequilateral, with more or less pointed ends. *Asteromella* spermatial forms are typical. Representative species: the common polyphagous *M. subradians*.

Section *Longispora*: cylindrical asci with aggregated, thin-walled, long and slender ascospores that are rarely constricted at the septum and mostly equilateral, long but slender ascospores, characteristically with rounded upper and pointed lower ends. Anamorphs: *Phloeospora* or *Septoria s. lat.* Representative species: *M. eryngii* (with short spores), *M. latebrosa* and *M. populi* (with longer spores). The phylogenetic position of *Sphaerulina*, which differs by having additional ascospore septa, still needs to be resolved.

Section *Fusispora*: pyriform asci and irregularly arranged, thin-walled ascospores that are rarely constricted at the septum and mostly equilateral, fusiform, pointed ascospores. Anamorphs have not been proven. Representative species: the common *M. lineolata* on *Poaceae*.

Section *Plaga*: (incl. Section *Macula*) incorporates endophytic species sporulating on leaf spots, many of which are described as plant pathogens. This section is characterised by obovoid to ellipsoidal or cylindrical asci, small to medium sized ascospores, fusiform to obovoid with rounded ends. Many species have been described in this section, the majority of which originate from warm-temperate and tropical areas. Anamorphs include *Kirramyces*, *Passalora*, *Phaeophleospora*, *Pseudocercospora*, *Pseudocercospora*, *Sonderhenia* and *Stenella*. Several representative species are listed by Crous (1998) on *Eucalyptus*.

Section *Cymadothea*: This section is now accepted as the genus *Polytrincium* (*Cymadothea* teleomorph) (Simon *et al.*, 2009). *Cymadothea* has superficial ascomata situated on a stroma of pseudoparenchymatal cells, and ascospores that can become pale brown with age. The *Polytrincium* anamorph is quite

unique, forming fascicles with conidiogenous loci arranged along the one side of the conidiogenous cells, with slightly darkened scars. Representative species: the genus is monotypic, with *P. trifolii* occurring on *Trifolium*.

Von Arx (1949) proposed separating species with separate ascomata immersed within the host tissue, and those with ascomata occurring in pseudoparenchymatous stromata. This idea certainly has merit, but too few taxa in the latter category have been subjected to DNA analyses to fully test this proposal. The original hypothesis of separating species with pigmented ascospores into *Phaeosphaerella*, while retaining those with hyaline ascospores in *Mycosphaerella*, should also be reinvestigated. This separation was also followed by Tomilin (1979). However, Müller and von Arx (1962) found that the type species of *Phaeosphaerella*, *P. maculosa* was identical to *Venturia macularis*. A new generic name would thus have to be introduced for species with pigmented ascospores. Species with hyaline and slightly pigmented ascospores are currently retained in *Mycosphaerella*, though some are now placed in *Teratosphaeria* (see below). Although ascospore germination patterns have thus far only been used at species level (Crous, 1998; Crous *et al.*, 2004a), many species with ascospores that turn dark and verruculose during germination (Crous *et al.*, 1993a,b; Crous and Wingfield 1996; Crous *et al.*, 2008a,b) have in fact been shown to belong to *Teratosphaeria*, not *Mycosphaerella*, suggesting that this character may have value at the generic level as well.

Klebahn (1918) and Laibach (1922) proposed that species be classified in different genera according to their anamorphs, and proposed *Septorisphaerella* (*Septoria* anamorphs), *Ramularisphaerella* (*Ramularia* anamorphs), *Cercosphaerella* (*Cercospora* anamorphs) and *Ovosphaerella* (*Ovularia* anamorphs = *Ramularia* fide Braun 1998). This approach was not accepted by subsequent workers. Von Arx (1983) stated that the presence or absence of anamorphs should not be used to separate genera, subgenera or sections in *Mycosphaerella*. Crous (1998) suggested that anamorph morphology, rather than features such as ascus and ascospore shape be used to

separate genera within *Mycosphaerella*, though initial DNA phylogenies based on ITS sequence data refuted this (Crous *et al.*, 2000; Goodwin *et al.*, 2001; but see below). Although Sutton and Hennebert (1994) suggested that different anamorph conidiogenous events and conidiomatal types could prove useful in grouping species at some subgeneric level, the presence of synanamorphs (Crous *et al.*, 2007a,c), and general plasticity observed in conidiogenesis and conidiomatal structure when studied in culture, suggests that these characters should be used with caution.

Barr (1996) placed two species occurring on pine needles in a new genus, *Eruptio* (*Lecanosticta* and *Dothistroma* anamorphs) based on their elongate, erumpent ascostromata that open via schizogenously formed ostioles. The taxa presently accommodated in *Eruptio* are, however, not congeneric, and this genus will have to be evaluated further in future studies.

Although *Sphaerulina* was established to accommodate taxa with primarily 3-septate ascospores, Crous *et al.* (2003b) showed that some elements of ‘*Sphaerulina*’ clearly belong in *Mycosphaerella*, and that ascospore septation is not as definitive as previously thought. The most significant finding, however, was that *Mycosphaerella* is an assemblage of numerous genera that are morphologically similar. These genera are more easily separated based on their anamorphs (Crous, 1998; Crous *et al.*, 2007a), though the same anamorph morphology could also evolve in more than one lineage (genus), making morphological identifications cumbersome in certain groups.

The separation of *Davidiella* teleomorphs (Braun *et al.*, 2003) with their angular lumens, remnants of hamathecial tissue, and *Cladosporium s.str.* anamorphs was a significant step in redefining *Mycosphaerella*. The next was the separation of *Teratosphaeria* from *Mycosphaerella* (Crous *et al.*, 2007a). Species of *Teratosphaeria* are distinguished from *Mycosphaerella* by frequently having hamathecial remnants, a multi-layered ascal endotunica, and ascospores with sheaths that frequently turn brown while still in their asci. Anamorph genera were shown to also not overlap between *Mycosphaerella* and *Teratosphaeria*. In a recent paper by Schoch *et al.* (2006), further

support was provided for the separation of the *Teratosphaeriaceae* from the *Mycosphaerellaceae* and *Davidiellaceae*, while all families were shown to be members of the *Capnodiales* (*Dothideomycetes*).

The genus *Mycosphaerella* s.str.: *Ascomata* are submerged, separate, somewhat erumpent, small, simple, globose, black, with walls of 2–4 layers of textura angularis. *Ostioles* are central, frequently lined with periphyses. *Asci* are bitunicate, fasciculate, lacking hamathecial filaments. *Ascospores* are 1-septate, hyaline, lacking appendages and sheaths. *Anamorphs* are accommodated in *Ramularia*.

Contemporary taxonomy of *Mycosphaerella* is based on a range of characters, including symptoms on host plants, morphological characters of both anamorphs and teleomorphs, cultural characteristics, and DNA phylogeny (Crous, 1998; Stewart *et al.*, 1999; Crous *et al.*, 2000).

Symptomatology

Lesions vary in shape from being angular to circular or irregular, and in size from specks to spots or larger coalescing blotches, causing a distortion of the leaf lamina. Lesions also vary in colour at different stages of development, and can be smooth and amphigenous, or corky and not extending through the lamina (Fig. 1). Borders of lesions can be raised, and frequently darker in colour, and margins can be absent, or vary from a chlorotic yellow to red or red-purple. Many *Mycosphaerella* spp. seem to occur only on foliage of defined age, namely on juvenile, intermediate or mature foliage. Lesions can also occur on fruit (spots or rot), or on twigs or stems, associated with dieback or cankers. Many species occur as symptomless endophytes, and are only observed to sporulate on plant debris.

Teleomorph characters

Ascomata of different species frequently vary in size between the larger- and smaller-spored species. Ascomatal distribution (upper or lower leaf surface), and aggregation (dense, sparse) and association with stromatic tissue, are very characteristic features among different taxa. Dimensions of the ascomatal wall cells tend to vary little among small- or large-spored species. However, some taxa have charac-

teristically thick walls, consisting of more layers than the general 3–4 cell layers observed in common species. Periphyses are commonly present, lining ostiolar canals, and their level of development varies among taxa. *Asci* are paraphysate, bitunicate, sessile, and formed in a fascicle, vary in shape from obovoid to narrowly or broadly ellipsoidal, or narrowly ellipsoidal to cylindrical (Fig. 2). *Ascospores* are mostly hyaline (*Mycosphaerella* s.str.), or slightly olivaceous in some taxa. They are usually bi- to triseriate in *asci* of large-spored species, or multiseriate in those with small-spored taxa. *Ascospores* can either be straight, curved, or both. They vary from being strongly guttulate to non-guttulate, thin- to thick-walled, and prominently, slightly or not constricted at the septum. *Ascospores* are mostly medianly 1-septate, but in some species the basal cell is slightly longer than the apical cell. The widest point in the ascospore can either be at the median septum, in the middle of the apical cell, or closer to the apex. The apical cell can also be asymmetrical. *Ascospores* vary in shape from narrowly ellipsoidal, fusoid-ellipsoidal, or obovoid. They taper from the middle toward both ends, or more prominently from the tip or middle of the upper cell toward the base.

Ascospore germination

Ascospore germination patterns represent a valuable feature to help distinguish morphologically similar species (Crous *et al.*, 1993a,b; Carnegie and Keane, 1994; Crous and Alfenas, 1995; Crous and Wingfield, 1996; Crous, 1998). Crous *et al.* (1991) studied ascospore germination by letting spores shoot from leaf lesions onto 2% malt extract plates. *Ascospores* were usually ejected within 24 hours, enabling germination patterns to be determined the following day. If left too long, ascospores from some faster growing species become totally distorted, clouding their germination patterns. For some species, germination is most characteristic at the very onset, whereas others tend to form lateral branches 24–48 hours after they have been shot onto the agar surface (Crous and Wingfield, 1996). These germination patterns have been found to be stable and reproducible, even when spores produced *in vitro* are germinated on agar. However, the patterns change when spores germinate in water or on different media, or are



Fig. 1. Disease symptoms associated with species of the *Mycosphaerella* complex. **a.** *Cercospora apii* leaf spots on *Apium graveolens* (M. Groenewald). **b.** *Cercospora beticola* spots on *Goniolimon tataricum* (S.G. Bobev). **c.** *Mycosphaerella sumatrensis* spot on *Eucalyptus*. **d.** *Teratosphaeria gauchensis* canker on *Eucalyptus* (M-N. Cortinas). **e.** red band needle blight of *Pinus* caused by *Dothistroma pini*. **f.** *Schizothyrium pomi* causing flyspeck of apple (J. Batzer). **g.** *T. verrucosa* spots on *Eucalyptus* (M.J. Wingfield). **h.** *Pseudocercospora lilacis* spot on *Ligustrum*. **i.** *T. fimbriata* spots on *Eucalyptus*. **j.** *Batcheloromyces protea* spot on *Protea*. **k.** *Mycosphaerella sphaerulinae* spot on *Eucalyptus*. **l.** *Passalora perplexa* blight of *Acacia* (M.J. Wingfield). **m.** *Mycosphaerella handelii* spot on *Rhododendron*. **n.** *Teratosphaeria parkii* spots on *Eucalyptus*. **o.** *Mycosphaerella fijiensis* spot on *Musa*. **p.** *Mycosphaerella* spots on *Musa*. **q.** Leaf spot with conidial cirri of *Septoria provincialis* on *Eucalyptus*; **r.** *Pseudocercospora griseola* causing angular leaf spot of *Phaseolus* (M.M. Liebenberg).



Fig. 2. Teleomorphs. **a.** Ascomata of *M. gracilis*. **b.** Squashed ascoma of a *Teratosphaeria* sp. on *Eucalyptus*. **c.** Asci as arranged inside ascoma of *M. acaciigena*. **d.** Asci of *Mycosphaerella* sp. occurring with *Cercospora acaciae-mangii*. **e.** Asci of *M. gracilis*. **f.** Asci of *T. toledana*. **g.** Asci of *Teratosphaeria* sp. on *Eucalyptus*. **h.** Asci of *T. pseudocryptica*. **i.** Ascus of *M. cussonia*. **j.** Asci of *Davidiella tassiana*. **k.** Ascus of *T. jonkershoekensis*. **l.** Ascospores of *M. longibasalis*. — Scale bars: a = 80; b, d–h = 40; c, i–l = 10 µm.

left for inordinately long after ascospore discharge. Standardisation to ensure reproducibility is, therefore, essential, and the time from discharge to observation must be carefully monitored. In studying the species occurring on *Eucalyptus*, Crous (1998) observed 14 different germination patterns (Fig. 3). Ascospores tend to become slightly swollen, or completely distorted, with one to several germ tubes emerging, growing at various angles to the long axis of the spore, remaining hyaline, or turning brown upon germination.

Colony growth in culture

Colony characteristics and ascospore morphology are generally consistent *in vitro*. *Mycosphaerella* species commonly have colonies that are various shades of grey or olivaceous-grey on MEA, though taxa with cream to brown or red colonies also exist, and some form diffuse pigments in the agar (Fig. 4). Distinct differences exist between species in growth rate, temperature requirements for growth (Groenewald *et al.*, 2005), presence of aerial mycelium and colony morphology (margins, colour, mycelium spreading or erumpent, chlamydospores, surface smooth or sectoried, crystal formation; Crous, 1998), formation of spermatogonia, (syn)anamorphs (Crous *et al.*, 2007a,c), and smooth or verrucose nature of creeping hyphae. Aerial hyphae can vary completely from those occurring on the agar surface in texture, pigmentation, width and constriction at septa.

Anamorphic *Mycosphaerella* in the post-Chupp era

Asteromella is now commonly accepted as the spermatial state that occurs with species of *Mycosphaerella* when studied in culture, or on host material (Crous and Wingfield, 1996), and it is possible that spermatial states have also been described as anamorphs in genera such as *Ascochyta*, *Asteroma* and *Phoma*. Most attention to date has been directed towards the hyphomycetous anamorphs of *Mycosphaerella*. Crous *et al.* (2000, 2001) listed 30 anamorph genera which had been linked to *Mycosphaerella* (Figs 5, 6). Since then, many have been reduced to synonymy, namely *Uwebraunia* and *Dissoconium* (Crous *et al.*, 2004a),

Paracercospora and *Pseudocercospora* (Stewart *et al.*, 1999), *Cercostigmia*, *Stigmia*, *Phaeoisariopsis* and *Pseudocercospora* (Crous *et al.*, 2004b, 2006b; Braun and Crous, 2006), *Ovularia*, *Ophiocladium* and *Ramularia* (Sutton and Waller, 1988; Braun, 1998; Crous *et al.*, 2000, 2001).

Several anamorph genera have been newly introduced to accommodate *Mycosphaerella* anamorphs, or anamorphs formerly linked to *Mycosphaerella* (Table 1). These include *Lecanosticta*, *Lecanostictopsis* (Sutton and Crous, 1997; Verkley and Priest, 2000), *Xenostigmia* (Crous, 1998; Crous and Corlett, 1998), *Metulocladosporiella* (Crous *et al.*, 2006c), *Cladoriella* (Crous *et al.*, 2006d), *Helgardia* (Crous *et al.*, 2003a), *Batcheloromyces* (Taylor *et al.*, 2003), *Cibiessia*, *Phaeothecoidea*, (Crous *et al.*, 2007c), *Pseudotaeniolina*, *Devriesia*, *Capnobotryella*, *Hortaea*, *Readeriella*, *Staninwardia*, *Penidiella* (Summerell *et al.*, 2006; Crous *et al.*, 2007a,c), *Rachicladosporium*, *Toxicocladosporium*, *Verrucocladosporium*, *Ochrocladosporium*, *Rhizocladosporium*, *Graphiopsis* (= *Dichocladosporium*) (Schubert *et al.*, 2007a; Braun *et al.*, 2008), *Zasmidium*, *Ramichloridium*, *Periconiella* (Arzanlou *et al.*, 2007b), *Dothistroma* (Barnes *et al.*, 2004; Groenewald *et al.*, 2007), *Parapericoniella*, *Digitopodium* (Heuchert *et al.*, 2005), *Trochophora*, *Verrucisporota* (Beilharz and Pascoe, 2002; Crous *et al.*, 2009a), *Baudoinia* (Scott *et al.*, 2007), *Ramulispora* (Crous *et al.*, 2003a), and *Colletogloeum* will soon be introduced (Crous *et al.*, unpubl. data).

Considerably fewer genera of coelomycetes have been linked to *Mycosphaerella*. Although the *Septoria* – *Phloeospora* – *Stagonospora* complex has not yet been resolved (Verkley and Priest, 2000), other coelomycetous genera associated with the *Mycosphaerella* complex include *Lecanosticta* (Sutton and Crous, 1997; Verkley and Priest, 2000), *Phaeophleospora* (Crous *et al.*, 1997; Crous, 1998), *Colletogloeopsis* (Crous and Wingfield, 1997), *Kirramyces* (Walker *et al.*, 1992; Andjic *et al.*, 2007), *Clypeispora* (Ramaley, 1991), *Sonderhenia* (Park and Keane, 1984; Swart and Walker, 1988), *Readeriella*, *Staninwardia* and *Nothostrasseria* (Summerell *et al.*, 2006; Crous *et al.*, 2007a).

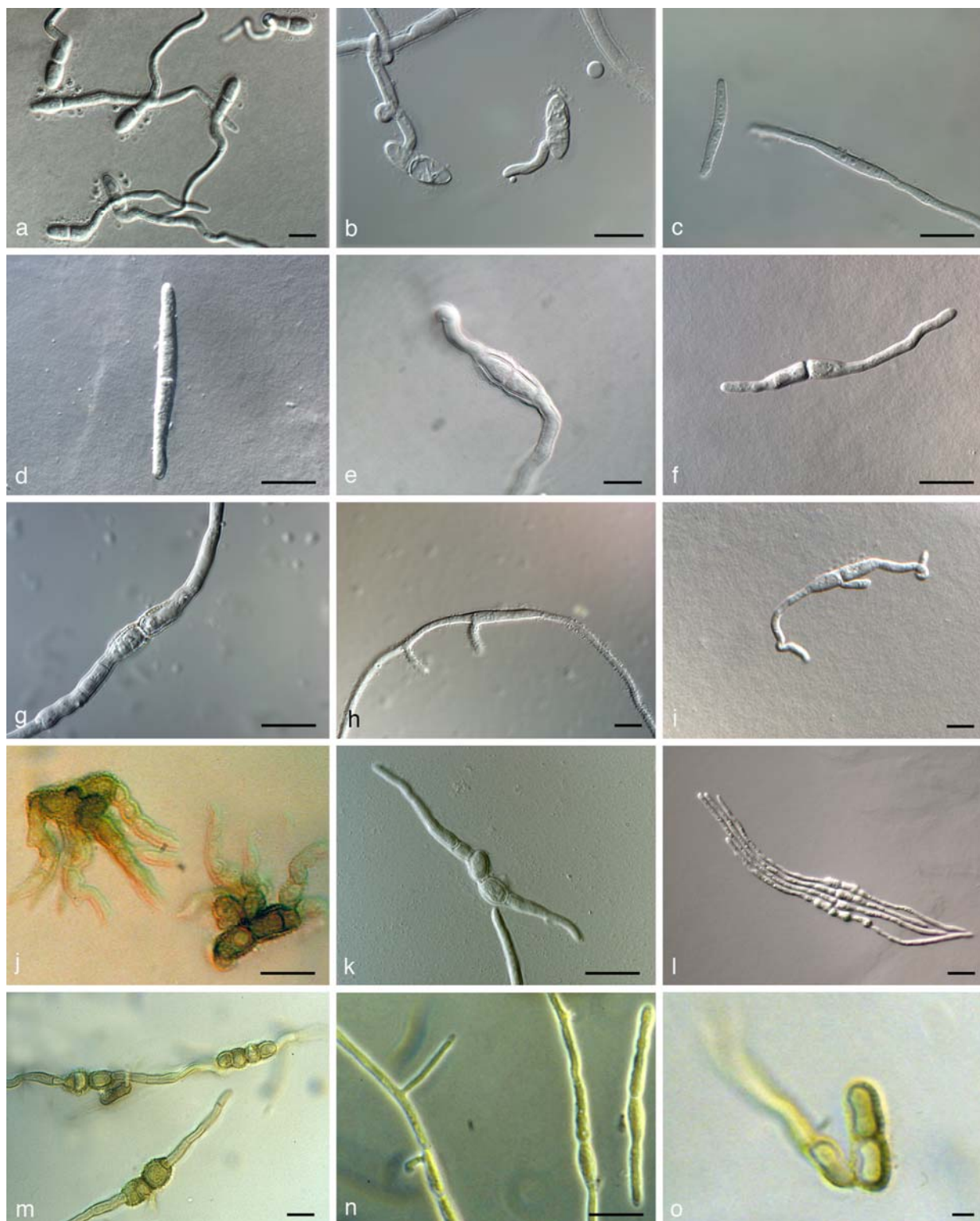


Fig. 3. Ascospore germination patterns sensu Crous (1998). **a.** *Teratosphaeria cryptica* (Type A). **b.** *Mycosphaerella mozambica* (Type A). **c.** *M. gracilis* (Type B). **d.** *M. cussonia* (Type B). **e.** *Davidiella tassiana* (Type C). **f.** *T. alistairii* (Type C). **g.** *T. jonkershoekensis* (Type G). **h.** *M. elaeocarpi* (Type H). **i.** *M. graminicola* (Type D). **j.** *T. suberosa* (Type E). **k.** *M. parkiiaffinis* (Type F). **l.** *T. nubilosa* (Type F). **m.** *T. africana* (Type G). **n.** *M. colombiensis* (Type J). **o.** *T. parva* (Type N). — Scale bars = 10 μ m.

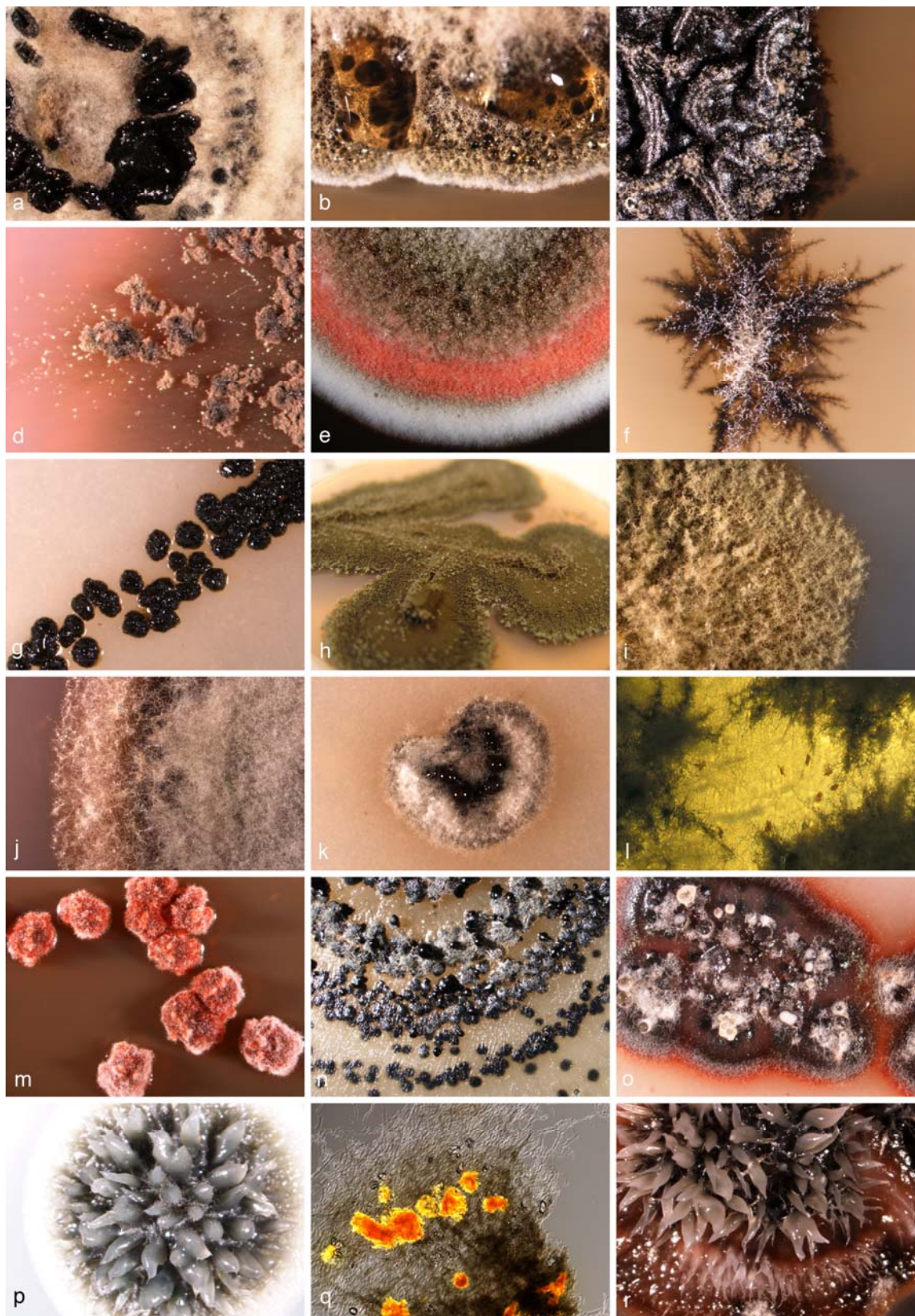


Fig. 4. Species of the *Mycosphaerella* complex in culture. **a.** *Teratosphaeria molleriana* on oatmeal agar (OA); **b.** *Stenella eucalypti* on malt extract agar (MEA); **c.** *Readeriella brunneotingens* on MEA; **d.** *Cibiessia minutispora* on OA; **e.** *Cercospora* sp. on MEA; **f.** *Cercospora ipomoeae* on OA; **g.** *Phaeothecoidea proteae* on OA; **h.** *Cibiessia dimorphospora* on PDA; **i.** *Teratosphaeria majorizuluensis* on MEA; **j.** *Teratosphaeria dendritica* on OA; **k.** *Phaeophleospora stonei* on OA; **l.** *Mycosphaerella heimii* on water agar (note crystals); **m.** *Ramularia* sp. on MEA; **n.** *Readeriella eucalypti* on OA; **o.** *Septoria* sp. on OA; **p.** *Teratosphaeria* sp. on OA; **q.** *Teratosphaeria alistairii* on potato-dextrose agar (note cysts); **r.** *Septoria proteae* on OA.

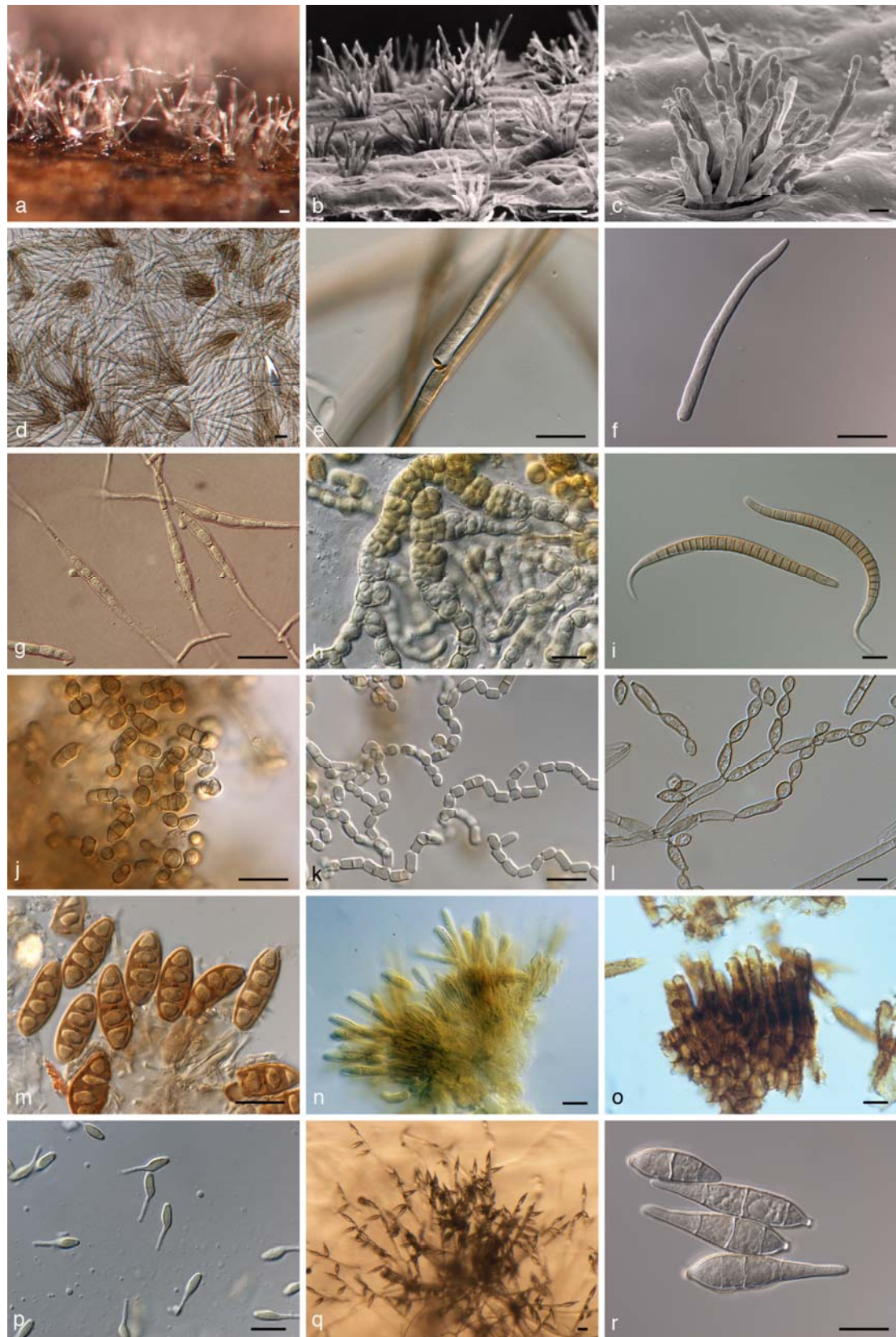


Fig. 5. Anamorphs associated with the *Mycosphaerella* complex. **a–d.** Fascicles of *Cercospora zeina*. **e.** Conidiophore giving rise to conidium of *Cercospora* sp. **f.** Conidium of *Cercospora* sp. **g.** Macro and microconidia of *Dissoconium dekkeri* anamorph of *M. lateralis*. **h.** Hyphae with endoconidia of *Phaeothecoidea eucalypti*. **i.** Conidia of *Phaeophleospora eugeniae*. **j.** Conidia of *Batcheloromyces leucadendri*. **k.** Conidia of *Cibiessia dimorphospora*. **l.** Conidiophore of *Cladosporium sphaerospermum*. **m.** Conidia of *Sonderhenia eucalypticola* anamorph of *M. walkeri*. **n.** Conidiophores of *Pseudocercospora punctata* anamorph of *M. syzygii*. **o.** Conidiophores of *Lecanostictopsis syzygii*. **p.** Conidia of *Nothotrasseria dendritica* anamorph of *T. dendritica*. **q.** *Passalora* sp. sporulating in culture. **r.** Pigmented conidia of *Passalora* sp. with thickened hila. — Scale bars = 10 µm, except d = 40 µm.

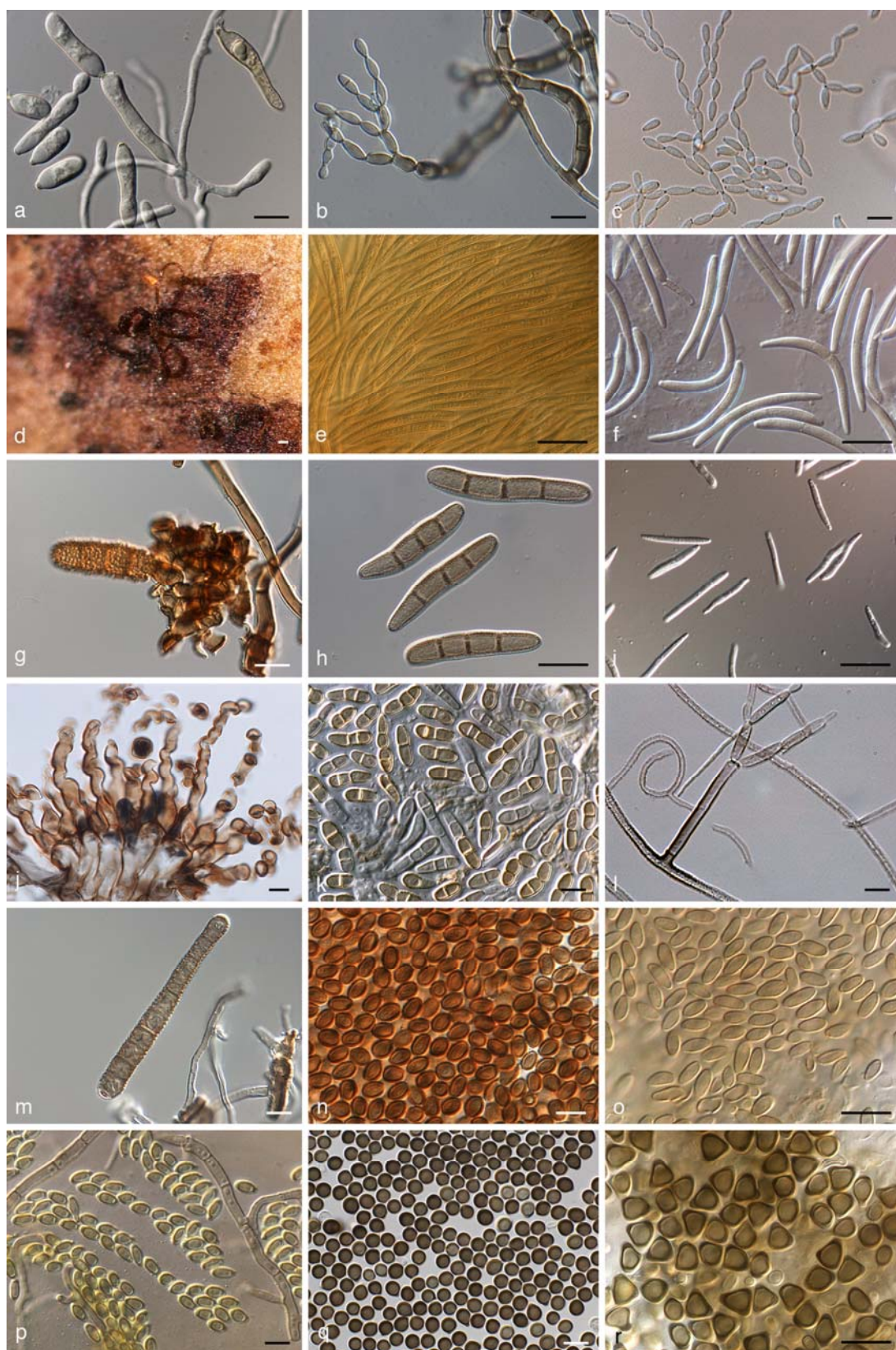


Fig. 6. Anamorphs associated with the *Mycosphaerella* complex. **a.** Conidia of *Passalora fulva*. **b.** Conidiophore of *Penidiella* anamorph of *Teratosphaeria encephalarti*. **c.** Conidia of *Ramularia eucalypti*. **d.** Exuding cirrus of *Kirramyces* anamorph of *T. suttonii*. **e.** Conidia of *Kirramyces destructans*. **f.** Conidia of *K. eucalypti*. **g.** Conidium of *Stigmina eucalypti*. **h.** Conidia of *Sonderhenia eucalyptorum* anamorph of *M. swartii*. **i.** Conidia of *Septoria eucalyptorum*. **j.** Conidiophore of *Polythrincium trifolii*, anamorph of *Cymadothea trifolii*. **k.** Conidia of *Staninwardia suttonii*. **l.** Conidiophore of *Stenella* sp. **m.** Conidium of *Verrucisporota grevilleae*. **n.** Conidia of *T. verrucosa*. **o.** Conidia of *T. gauchensis*. **p.** Conidia of *Readeriella readeriellophora*. **q.** Conidia of *R. eucalypti*. **r.** Conidia of *R. mirabilis*. — Scale bars = 10 µm, except d = 40 µm.

Table 1. Anamorph genera linked to *Mycosphaerellaceae* (M) and *Teratosphaeriaceae* (T)¹.

| Genus | Conidiomata ² | Synanamorph | | | Conidia | | Loci ⁵ | Arrangement ⁶ | Mycelium ⁷ | Reference |
|-----------------------------|--------------------------|-------------------------------|----------------------------|-------------------------------|--------------------|-------|-------------------|--------------------------|-----------------------|---|
| | | | Proliferation ³ | Colour ⁴ | Conidial septation | | | | | |
| <i>Batcheloromyces</i> (M) | S | <i>Catenulostroma</i> -like | P | P | 0–3 | I | S,C | I,E | | Taylor <i>et al.</i> (2003) |
| <i>Baudoinia</i> (T) | Ph | – | Ph | P | 0–1 | I | C | E | | Scott <i>et al.</i> (2007) |
| <i>Capnobotryella</i> (T) | Ph | Endoconidia | Ph | P | 0–1 | I | C | <u>E</u> | | Sugiyama and Amano (1987) |
| <i>Catenulostroma</i> (T) | A,S,F | – | Ph | P | 0-multi | I | S,C | I,E | | Crous <i>et al.</i> (2007a) |
| <i>Cercospora</i> (M) | F | – | S | H (conidia) P (conidioph.) | 0-multi | T,D,R | S | <u>I</u> | | Crous and Braun (2003) |
| <i>Cercosporella</i> (M) | F | – | S | H | multi | T,R | S | I | | Braun (1995) |
| <i>Cibiessia</i> (T) | Ph | <i>Readeriella</i> -like | Ph | P | 1–3 | I | C | I,E | | Crous <i>et al.</i> (2007c) |
| <i>Clypeispora</i> (?) | P | – | M | H | 0 | I | S | I | | Ramaley (1991) |
| <i>Colletogloeopsis</i> (T) | A/P | – | P,S | P | 0–1 | I | S | I,E | | Crous and Wingfield (1997) |
| <i>Davisoniella</i> (T) | M | Coelomycete | P | P | 0 | I | S | I | | Crous <i>et al.</i> (2006e) |
| <i>Devriesia</i> (T) | Sol | Chlamydospores | S | P | 0–3 | T,D | C | E | | Seifert <i>et al.</i> (2004) |
| <i>Dothistroma</i> (M) | A | – | P,S | H | 1–5 | I | S | I | | Barnes <i>et al.</i> (2004) |
| <i>Hortaea</i> (T) | Sol | – | P,M | H (conidia) P (hyphae) | 0–2 | I | S | I,E | | Bonifaz <i>et al.</i> (2008); Plemenitaš <i>et al.</i> (2008) |
| <i>Kirramyces</i> (T) | P | <i>Pseudocercospora</i> -like | P,S | P | 0-multi | I | S | I | | Andjic <i>et al.</i> (2007) |

Table 1 (continued). Anamorph genera linked to *Mycosphaerellaceae* (M) and *Teratosphaeriaceae* (T)¹.

| Genus | Conidiomata ² | Synanamorph | | | Conidia | Loci ⁵ | Arrangement ⁶ | Mycelium ⁷ | Reference |
|--------------------------------|--------------------------|-----------------|----------------------------|---------------------|--------------------|-------------------|--------------------------|-----------------------|--------------------------------|
| | | | Proliferation ³ | Colour ⁴ | Conidial septation | | | | |
| <i>Lecanosticta</i> (M) | A | – | P | P | 0-multi | I | S | I | Suto and Ougi (1998) |
| <i>Miuraea</i> (M) | F,Sol | – | S | H,P | muriform, multi | I | S | I,E | von Arx (1983) |
| <i>Nothostrasseria</i> (T) | P | – | M | P | 0 | I | S | I | Crous <i>et al.</i> (2007c) |
| <i>Passalora</i> (M) | F,S,Sol | – | S | P | 0-multi | T,D,R | S,C | I,E | Crous and Braun (2003) |
| <i>Penidiella</i> (T) | Sol,F,Syn | – | S | P | 0–1 | I or T,D | C | I,E | Crous <i>et al.</i> (2007a) |
| <i>Periconiella</i> (M) | Sol | – | S | P | 0-multi | T,D | C | I,E | Arzanlou <i>et al.</i> (2007b) |
| <i>Phaeophleospora</i> (M) | P | – | P | P | 0-multi | I | S | I | Crous <i>et al.</i> (1997) |
| <i>Phloeospora</i> (M) | A | – | S | H | multi | I | S | I | Sivanesan (1984) |
| <i>Phaeothecoidea</i> (T) | En | – | En | P | 0–2 | I | S | I,E | Crous <i>et al.</i> (2007c) |
| <i>Pseudocercospora</i> (M) | F,S,Sol,Syn | <i>Stigmina</i> | S | P | 1-multi | I | S,C | I,E | Deighton (1976) |
| <i>Pseudocercosporella</i> (M) | F,S,Sol | – | S | H | 1-multi | I | S,C | I,E | Braun (1998) |
| <i>Pseudotaeniolina</i> (T) | Sol | – | Ph | P | 0–2 | I | C | I,E | Crane and Schoknecht (1986) |
| <i>Ramichloridium</i> (M) | Sol | – | S | P | 0–1 | D | S | I,E | Arzanlou <i>et al.</i> (2007b) |
| <i>Ramularia</i> (M) | F,S,Sol | – | S | H | 0–5 | T,D,R | S,C | I,E | Braun (1998) |
| <i>Ramulispora</i> (M) | S | Chlamydospores | S | H | 0-multi | I | S | I,E | Crous <i>et al.</i> (2003a) |
| <i>Readeriella</i> (T) | P | – | P,M | P | 0 | I | S | I | Crous <i>et al.</i> (2007a) |

Table 1 (continued). Anamorph genera linked to *Mycosphaerellaceae* (M) and *Teratosphaeriaceae* (T)¹.

| Genus | Conidiomata ² | Synanamorph | Proliferation ³ | Colour ⁴ | Conidia Conidial septation | Loci ⁵ | Arrangement ⁶ | Mycelium ⁷ | Reference |
|---------------------------|--------------------------|--------------------------|----------------------------|---------------------|----------------------------------|-------------------|--------------------------|-----------------------|---------------------------------|
| <i>Septoria</i> (M) | P/A | – | S | H | 1-multi | I | S | I | Von Arx (1983) |
| <i>Sonderhenia</i> (M) | P | – | P | P | 0–5 | I | S | I | Swart and Walker (1988) |
| <i>Staninwardia</i> (T) | A | – | P | P | 1–2 | I | C | I | Summerbell <i>et al.</i> (2006) |
| <i>Stenella</i> (T) | F,Sol | <i>Scytalidium</i> -like | S | P | 0-multi | T,D,R | S,C | I,E | Sivanesan (1984) |
| <i>Trochophora</i> (M) | F,Sol | – | S | P | 3 | I | S | I,E | Zhao <i>et al.</i> (2007) |
| <i>Verrucisporota</i> (M) | F,Sol | – | S | P | 0-multi | T,D,R | S,C | I,E | Crous <i>et al.</i> (2009a) |
| <i>Zasmidium</i> (M) | F,Sol | – | S | P | 0-multi | T,D,R | S,C | I,E | Arzanlou <i>et al.</i> (2007b) |

¹*Asteromella* spermatial states have also been described in *Ascochyta*, *Asteroma*, *Phyllosticta* and *Phoma*. Excluded genera are *Dissoconium* (= *Uwebraunia*), *Cladosporium* (*Davidiellaceae*), *Thecogonia* (*Helotiales*), *Xenostigmina* (*Pleosporales*). *Mycovellosiella* and *Phaeoramularia* are treated as synonyms of *Passalora*; *Phaeoisariopsis*, *Paracercospora* and *Stigmina* as synonyms of *Pseudocercospora*.

²Fasciculate (F), sporodochial (S), solitary (Sol), pycnidial (P), acervular (A), synnematosus (Syn), phragmosporous (Ph), hyphae with endoconidia (En), multilocular (M).

³Sympodial (S), percurrent (P), monoblastic, determinate (M), phragmospores (Ph), endoconidia (En).

⁴Hyaline (H), pigmented (P).

⁵Thickened (T), darkened (D), refractive (R), protruding (P), inconspicuous (I).

⁶Solitary (S), chains (C).

⁷Internal (I), external (E).

Most hyphomycetous genera linked to *Mycosphaerella* have traditionally been dealt with as part of the cercosporoid complex (Table 1) (Braun, 1995, 1998; Crous and Braun, 2003). These anamorph genera have been separated into more 'natural' or recognisable units based on features such as the presence or absence of superficial mycelium, and its texture. Conidiophore characteristics include arrangement, branching, pigmentation, conidiogenous cell placement, proliferation, scar type and conidial formation, shape, septation, wall texture and pigmentation. In most cases cercosporoid fungi have been treated as asexual fungi, and teleomorphs have been confirmed for only a few species (Braun and Crous, 2007; Kirschner and Chen, 2007; Nakashima *et al.*, 2007). As is the case with their *Mycosphaerella* teleomorphs, cercosporoid fungi are associated with leaf spots, but can also cause necrotic lesions on flowers, fruits, bracts, seeds and pedicels of numerous hosts in most climatic regions. Furthermore, other than important pathogens of major agricultural crops, cercosporoid fungi are also known to be hyperparasitic to other plant pathogenic fungi (Shin and Kim, 2001), and are also important as biocontrol agents of alien weeds (Morris and Crous, 1994; Den Breeÿen *et al.*, 2006; Pereira *et al.*, 2007).

Chupp (1954) proposed a broad concept for the genus *Cercospora*, simply recording if hila were thickened or not, and if conidia were pigmented, single or in chains. As very little was known about the sexual states and relationships of cercosporoid fungi, Chupp chose a more practical approach by retaining all these taxa in *Cercospora*. Subsequent workers such as Deighton (1973, 1976, 1979, 1987, 1990) and Braun (1995, 1998) divided the *Cercospora*-complex into smaller, more morphologically similar units based on a combination of characters including conidiomatal structure (sporodochia, synnemata), mycelium (presence or absence of superficial mycelium and texture thereof), conidiophores (arrangement, branching, pigmentation and ornamentation), conidiogenous cells (placement, proliferation and scar type) and conidia (formation, shape, septation, ornamentation, pigmentation and catenulation).

The abandonment of the 'Chupp concept' has resulted in close to 50 genera being recognised in this complex (Braun, 1995; Crous and Braun, 2003). One of the reasons for this was the strict interpretation of the numerous conidiogenous events as defined by Sutton and Hennebert (1994), as well as the additional characters discussed above. Several anamorph genera have been found to have species with conidiomata varying from mononematous, scattered conidiophores to sporodochia with a basal stroma, or from pycnidia to sporodochia and synnemata. Based on similar observations Sutton (1980) and Nag Raj (1993) saw the need to abandon the distinction between hyphomycetes and coelomycetes, as acervuli were frequently found to form a continuum with more stromatic, sporodochial forms. If this plasticity is taken into consideration when examining the 23 anamorph genera accepted by Crous *et al.* (2000), many appear superfluous. However, recent phylogenetic studies have shown that many of the current generic concepts are represented as paraphyletic clades within some families in the *Capnodiales* (e.g. *Mycosphaerellaceae* or *Teratosphaeriaceae*) (Crous *et al.*, 2007a; Arzanlou *et al.*, 2007b), suggesting that some of these anamorph concepts still represent more than one genus. In other families in the order, such as *Schizothyriaceae* (Batzler *et al.*, 2008) and *Davidiellaceae* (Crous *et al.*, 2007b; Schubert *et al.*, 2007a,b), this appears not to be the case, and the teleomorph is thus far linked to a single anamorph.

Characters such as the presence or absence of superficial mycelium, the formation of stromata, conidiomatal structure (conidiophores solitary, fasciculate to synnemata, sporodochia to pycnidia and acervuli), conidial shape, size and septation (even eusepta vs. distosepta), as well as solitary vs. catenate conidia, saprobic, hyperparasitic and phytopathogenic habit, were rejected as single characters at the generic level by Crous and Braun (2003). These recent findings suggest, however, that all these characters again need to be re-evaluated in light of novel DNA data.

From these studies it was shown that most of these cercosporoid genera (with the

possible exception of *Cercospora* and *Ramularia*), evolved more than once in the *Mycosphaerellaceae*. The majority of the 'anamorph genera' linked to *Mycosphaerella* in the broad sense, therefore, represent several phylogenetic units, e.g. *Pseudocercospora*, *Passalora*, *Septoria* and *Stenella*. To reduce the number of novel anamorph genera being introduced, Crous *et al.* (2007a) accepted the concept of paraphyletic anamorph genera within a specific family. This approach, however, has not been widely accepted, which means that many more genera will be introduced as *Mycosphaerella* is further separated into natural units. Teleomorph, as well as anamorph characters will have to be re-evaluated. The characters used by Crous and Braun (2003) to delineate anamorph genera still apply, namely the structure of conidiogenous loci (scars) and hila, and the presence or absence of pigmentation in conidiophores and conidia. In cases where genera are paraphyletic, however, these characters require further refinement.

DNA phylogeny of *Mycosphaerella* species complexes on different hosts

Although the *Mycosphaerella* complex accommodated several thousand species, very few are known from culture. Largely due to the lack of cultures, the first DNA phylogeny paper on *Mycosphaerella* was that published by Stewart *et al.* (1999). Based on ITS phylogenetic data, subsequent workers (Crous *et al.*, 1999; Goodwin *et al.*, 2001) concluded that *Mycosphaerella* was monophyletic. This research was continued by Crous *et al.* (2000, 2001), wherein the anamorph concepts were re-evaluated, and based on the limited number of species available, most genera were shown to represent well-defined clades within *Mycosphaerella*. Once multi-gene data were employed (Hunter *et al.*, 2006; Schoch *et al.*, 2006; Crous *et al.*, 2007a,b; Arzanlou *et al.*, 2007b; Batzer *et al.*, 2008), *Mycosphaerella* was shown to be polyphyletic, and the well-defined anamorph genera were shown to have evolved in several clades, within and outside the order, suggesting that in many cases the generic circumscriptions would have to be revised.

DNA phylogenetic techniques further revealed that for all hosts investigated, there were a surprisingly high number of novel species. This was true for example on *Citrus* (Pretorius *et al.*, 2003), *Acacia* (Crous *et al.*, 2004b), *Chromolaena* (Den Breejën *et al.*, 2006), *Eucalyptus* (Crous *et al.*, 2004a, 2006e, 2007c; Cheewangkoon *et al.*, 2008), *Zea mays* (Crous *et al.*, 2006a), *Encephalartos* (Crous *et al.*, 2008b), *Proteaceae* (Crous *et al.*, 2008a), and *Musa* (Arzanlou *et al.*, 2008), to name but a few. From these various studies, the same pattern emerged, namely that many morphologically similar species occur on the same host, and that based on morphology alone, it is typically very difficult or impossible to distinguish them. What this in turn implies for species numbers, is that in coming years there will be a significant expansion in the number of novel taxa described, and that the *Mycosphaerella* complex accommodates far more species than the 10 000 taxa described to date.

Host-specificity in *Mycosphaerella*

A significant problem pertaining to the taxonomy of *Mycosphaerella* is the degree of host-specificity of the various species. Most species are still defined based on host, and they are assumed to be host-specific or restricted at least to a family of phanerogamic plants (Chupp, 1954; Corlett, 1991; Braun, 1995). However, the tenability of many species may be called into question because some taxa, including *M. punctiformis*, the type species of *Mycosphaerella*, have been shown to be non host-specific (Verkley *et al.*, 2004).

Although many may be host-specific, some *Mycosphaerella* species are able to colonise different and even unrelated hosts. In some cases this appears to be due to the endophytic nature of these fungi (Crous, 1998; Verkley *et al.*, 2004), while in others species appear to actively undergo host shifts in the process of locating their ideal hosts (Crous *et al.*, 2004b; Crous and Groenewald, 2005). Crous *et al.* (2008a) reported that many host-specific necrotrophic pathogenic species of *Mycosphaerella* and *Teratosphaeria* appeared to also exhibit a facultative saprobic behaviour. It was concluded, therefore, that the definitions of 'necrotroph' or 'saprobe' do not clearly

define all species of *Mycosphaerella* and *Teratosphaeria*, as some have obviously retained the ability to also grow on dead tissue when they lose the connection to their real host.

In many instances, species of *Mycosphaerella* with wide host ranges are morphologically indistinguishable, such as those in the *Cercospora apii* complex (Groenewald *et al.*, 2005). In the genus *Cercospora*, however, several species are known that are highly host-specific, and thus there appears to be no general rule regarding this ecological trait (Groenewald *et al.*, 2006a). The fact that many species can co-occur in the same lesion or leaf spot, the so called 'co-occurrence phenomenon' (Crous *et al.*, 2009e), adds a new level of complexity to the isolation of these fungi, suggesting that only those strains that are fertile in culture, can be confirmed as representing the fungus studied on host material.

The majority of the plant pathogenic species of *Mycosphaerella* are thought to be host-specific (Goodwin *et al.*, 2001; Crous and Groenewald, 2005; Groenewald *et al.*, 2006a; Stukenbrock *et al.*, 2007), such as *M. fijiensis*, *M. musicola* and *M. eumusae* on banana (Arzanlou *et al.*, 2008) and *M. graminicola* on wheat (Stukenbrock *et al.*, 2007). In contrast, Crous *et al.* (2009e) reported several species to occur on multiple hosts, namely: *M. communis* (on *Eucalyptus* in South Africa, Spain, New Zealand, *Musa* in Trinidad, *Protea magnifica* in Australia), *M. konae* (*Leucospermum* in Hawaii, *Eucalyptus* in Thailand) (Crous *et al.*, 2007c), *M. marksii* (*Eucalyptus*, Australia, Bolivia, China, Ecuador, Ethiopia, Papua New Guinea, New Zealand, South Africa, Spain, Tanzania, Uruguay, *Leucadendron* on the Madeira Islands, and *Musa* in Mozambique) (Arzanlou *et al.*, 2008), *Teratosphaeria associata* (*Eucalyptus* and *Protea* in Australia) (Summerell *et al.*, 2006; Crous *et al.*, 2007c), *T. parva* (*Eucalyptus* in Australia, Chile, Ethiopia, Portugal, South Africa, Spain, and *Protea* in South Africa), *T. nubilosa* (*Eucalyptus* in Australia, New Zealand, Europe, South America, and *Acacia* in Thailand (Crous and Groenewald, 2005; Hunter *et al.*, 2009), and *Mycosphaerella citri* (*Musa* in Florida, *Acacia* in Thailand, and *Eucalyptus* in Vietnam, and *Aeglopsis*, *Citrus*, *Fortunella*, *Murraya*, and

Poncirus in North and South America, as well as Asia (Pretorius *et al.*, 2003; Crous *et al.*, 2004a,b; Crous and Groenewald, 2005, Burgess *et al.*, 2007).

The genetics of host-specificity of well-known pathogens such as *M. graminicola* has been studied extensively. For example, Banke *et al.* (2004) demonstrated that this species infects only bread wheat and durum wheat. Of interest, however, is the fact that based on certain genes, durum wheat isolates of *Mycosphaerella* clearly separate from bread wheat isolates (Groenewald and Crous, unpubl. data), suggesting that at some stage, these were either two distinct species infecting these hosts, or a single species currently undergoing speciation. Among the *Mycosphaerella* species infecting *Eucalyptus*, some species such as *Teratosphaeria cryptica* (syn. *M. cryptica*) have a broad host range and cause disease on 38 species across the *Eucalyptus* subgenera *Monocalyptus* and *Symphyomyrtus*, while *T. nubilosa* shows a more narrow host range, infecting only 12 *Eucalyptus* species and a few hybrids within the subgenus *Symphyomyrtus* (Park *et al.*, 2000; Maxwell *et al.*, 2005; Hunter *et al.*, 2009).

To successfully manage and control plant disease epidemics, a thorough understanding of the genetic variation and epidemiology of the causal agent(s) is required. Because *Mycosphaerella* species are morphologically similar, are not necessarily host-specific, and several species could co-occur in the same lesion, fungal identification and the choice of subsequent control regimes is not always straight forward. PCR-based techniques have in recent years contributed greatly to disease diagnosis and detection, and have also successfully been employed in the early detection of *Mycosphaerella* infections (Waalwijk *et al.*, 2004; Lievens *et al.*, 2005; Arzanlou *et al.*, 2007a).

Sex in *Mycosphaerella*

Ascomycetes with both a sexual and asexual reproductive cycle are haploid for the majority of their lifecycle (Heitman, 2006). During the short phase of sexual reproduction, they become dikaryotic, and diploid. Sexual reproduction in fungi involves meiosis, which is preceded by the fusion of two cells

(plasmogamy), followed by fusion of the two parental nuclei (karyogamy). Sexual reproduction together with mutation, recombination and natural selection are major forces that drive evolution (Heitman, 2006; Zhan *et al.*, 2007). It is generally accepted that asexual reproduction generates genetically identical clones, though the role of the parasexual cycle should not be underestimated, as anastomosis between different mycelial types will again influence the genetic makeup of eventual progeny. Conidia can result from fragmentation of hyphal cells (frequently observed in aerial mycelium of *Mycosphaerella* species), or via the production of conidia in naked (hyphomycete) or enclosed (coelomycete) fruiting bodies. Some species of *Mycosphaerella* form several anamorphs (synanamorphs), including hyphomycetes and coelomycetes (Crous *et al.*, 2007a), which enables them to better utilise changing environmental conditions, ensuring optimal spore production and dispersal. Detailed studies on sexual reproduction in fungi may provide better insights into genetic regulation and evolution of closely related taxa (Turgeon, 1998; McDonald and Linde, 2002; Conde-Ferraz *et al.*, 2007).

In the absence of selection pressure, asexual reproduction dominates populations. Changes in the availability of food resources, environmental conditions and other selection pressures favour a shift towards the sexual reproduction cycle (Heitman, 2006; Zhan *et al.*, 2007). In fungi like *Neurospora crassa*, individuals are hermaphrodites, producing both male and female reproductive structures. Sexual exchange of genetic material relies on the existence of simple cell recognition mechanisms that stimulate out-crossing. The term 'mating type' defines sexually compatible individuals. Heterothallism (self-sterility) occurs between two fungal strains with a compatible mating system. In contrast, homothallism (self-fertility) is where a single isolate can complete a successful sexual cycle. Pseudohomothallism or secondary homothallism occurs in some ascomycetes such as *Neurospora tetrasperma*, *Podospira anserina* and *Gelasinospora tetrasperma* (Merino *et al.*, 1996), where self-fertile ascospores carry nuclei of both mating types.

In fungi sexual development is controlled by mating type loci, which contain a number of genes which occupy a continuous region on a chromosome (Debuchy and Turgeon, 2006). In ascomycetes, sexual development is controlled by a single mating type locus (*MAT*). This mating type locus contains one of two forms of dissimilar sequences occupying the same chromosomal position, termed 'idiomorph' in fungal species with a heterothallic mating strategy (Metzenberg and Glass, 1990). Complementary idiomorph isolates are referred to as *MAT1-1* and *MAT1-2* mating strains (Turgeon and Yoder, 2000).

Although *Mycosphaerella* contains several thousand species, the mating behaviour of most species has not been resolved. Although some species have been observed to be either homo- or heterothallic, pseudohomothallism has not yet been reported for any *Mycosphaerella* species. By continuing the research done on the heterothallic mating system of *M. graminicola*, the mating behaviour of several apparently asexual species of *Cercospora* has been clarified (Groenewald *et al.*, 2006b). Much attention was also devoted to the elucidation of the mating systems active in the *Mycosphaerella* spp. occurring on banana (Conde-Ferraz *et al.*, 2007, Arzanlou *et al.*, in prep.). Using the same approach our knowledge for other *Mycosphaerella* species such as *Passalora fulva* (Stergiopoulos *et al.*, 2007), *Dothistroma septosporum* and *Dothistroma pini* (Groenewald *et al.*, 2007), and *Septoria passerinii* (Ware *et al.*, 2007) has also been extended. From these data it is clear that sex is active in several apparently asexual species of *Mycosphaerella*, and in species where the teleomorph is seldom observed.

How do we deal with the poly- and paraphyletic nature of *Mycosphaerella* and its anamorphs?

Early phylogenetic trees treating *Mycosphaerella* were based on ITS DNA sequence data, and these suggested that the genus is monophyletic (Crous *et al.*, 1999, 2000, 2001; Stewart *et al.*, 1999; Goodwin *et al.*, 2001). However, once additional loci were included in later analyses, it was shown that *Mycosphaerella* is polyphyletic (Hunter *et al.*, 2006;

Crous *et al.*, 2007a). This complex has in recent years been separated into *Davidiella* species with *Cladosporium* anamorphs (*Davidiellaceae*) (Braun *et al.*, 2003; Crous *et al.*, 2007b; Schubert *et al.*, 2007a,b; Zalar *et al.*, 2007; Dugan *et al.*, 2008), *Schizothyrium* species with *Zygophiala* anamorphs (*Schizothyriaceae*) (Batzler *et al.*, 2008), *Teratosphaeria* species with many anamorphs (*Teratosphaeriaceae*) (Crous *et al.*, 2007a,c), and *Mycosphaerella* species, also with numerous anamorph genera (*Mycosphaerellaceae*) (Crous and Braun, 2003), all belonging to the *Capnodiales* in the *Dothideomycetes* (Schoch *et al.*, 2006). Although *Davidiella* (*Cladosporium*) and *Schizothyrium* (*Zygophiala*) have a clear one to one relationship with anamorph genera, this is far from true for *Mycosphaerella* and *Teratosphaeria*, where the teleomorph morphology is relatively conserved throughout the two families. Here the same anamorph morphology has evolved in different clades, and in some cases also outside the families (Crous *et al.*, unpubl. data).

The option of accepting anamorph genera as paraphyletic concepts within the family and order (Arzanlou *et al.*, 2007b; Crous *et al.*, 2007a), has not been widely accepted by the scientific community (see Cortinas *et al.*, 2006; Andjic *et al.*, 2007; Crous *et al.*, 2007a, 2009e). This suggests that new generic names need to be provided for distinct lineages, and novel morphological characters identified to distinguish them (Essakhi *et al.*, 2008; Marincowitz *et al.* 2008; Nguyen and Seifert, 2008; Ruibal *et al.* 2008). In order to halt the unnecessary proliferation of generic names, it would thus be preferable to not continue with dual nomenclature, i.e. to use a single generic name per unambiguous phylogenetic lineage (Phillips *et al.*, 2007, Shenoy *et al.*, 2007). What this would imply, is that in several clades, where anamorph generic names are already available, preference will have to be given to anamorph names to try and achieve a more natural classification among the genera in these families. The greatest challenge, however, is to obtain a workable system, where morphological data can still be used to separate genera in what is presently seen as *Mycosphaerella s.str.*, as *Mycosphaerella s.str.* needs to be

confined to those taxa with *Ramularia* anamorphs.

The name *Mycosphaerella* has been confused in the past, and used widely for numerous genera not congeneric with the type species, *M. punctiformis*. If a single generic name is to be used for this '*Mycosphaerella*' clade, the older generic name, *Ramularia* (1833) may be preferable to *Mycosphaerella* (1884); thus *Ramularia endophylla*, not *M. punctiformis*, though both names would remain available, unless this change is implemented via some formal modification of the International Code of Botanical Nomenclature, giving preference to older generic names, irrespective of their sex.

Conclusions

The genus *Mycosphaerella* is commonly known as the largest genus of *Ascomycetes*, containing over 10,000 taxa if anamorph states are included. This assumption has been shown to be false, as *Mycosphaerella* is now known to be para- and polyphyletic (Crous *et al.*, 2009c,d). Furthermore, *Mycosphaerella s.str.* has been shown to be confined to taxa with *Ramularia* anamorphs, representing approximately 1000 species. In spite of this narrower circumscription of the genus, major taxonomic challenges remain unresolved. The teleomorph has been shown to be morphologically conserved throughout the family, while minute differences in anamorphs are indicative of different genera, complicated by the phenomenon of synanamorph states that commonly develop in culture, as well as on host material. Although much attention has in recent years been focused on hosts in the *Myrtaceae* and *Proteaceae*, a few preliminary studies on other hosts have indicated that most host plants have a rich representation of undescribed species in the *Mycosphaerella* complex. This aspect is further complicated by the fact that many of these taxa can co-occur on the same lesion (Crous *et al.*, 2009b,e), and have the ability to colonise non-host tissue, in an attempt to locate their ideal host to which they are pathogenic. Preliminary studies on their mating types and sexual behaviour have also indicated that some species are having cryptic sex, and that the

teleomorph is present, though seldom or not yet observed. These findings are also relevant for the import and export of agricultural and forestry produce, as for some species either one or both mating types have been introduced to different continents, suggesting that quarantine regulations also need to focus below the species level on clones and mating types.

References

- Andjic, V., Barber, P.A., Carnegie, A.J., Hardy, G.E. St J., Wingfield, M.J. and Burgess, T.I. (2007). Phylogenetic reassessment supports accommodation of *Phaeophleospora* and *Colletogloeopsis* from eucalypts in *Kirramyces*. *Mycological Research* 111: 1184-1198.
- Aptroot, A. (2006). *Mycosphaerella* and its anamorphs: 2. Conspectus of *Mycosphaerella*. CBS Biodiversity Series 5: 1-231.
- Arx, J.A. von. (1949). Beiträge zur Kenntnis der Gattung *Mycosphaerella*. *Sydowia* 3: 28-100.
- Arx, J.A. von. (1983). *Mycosphaerella* and its anamorphs. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series C, 86: 15-54.
- Arzanlou, M., Abeln, E.C.A., Kema, G.H.J., Waalwijk, C., Carlier, J., Vries, I. de, Guzmán, M. and Crous, P.W. (2007a). Molecular diagnostics for the Sigatoka disease complex of banana. *Phytopathology* 97: 1112-1118.
- Arzanlou, M., Groenewald, J.Z., Gams, W., Braun, U., Shin, H.-D. and Crous, P.W. (2007b). Phylogenetic and morphotaxonomic revision of *Ramichloridium* and allied genera. *Studies in Mycology* 58: 57-93.
- Arzanlou, M., Groenewald, J.Z., Fullerton, R.A., Abeln, E.C.A., Carlier, J., Zapater, M.-F., Buddenhagen, I.W., Viljoen, A. and Crous, P.W. (2008). Multiple gene genealogies and phenotypic characters differentiate several novel species of *Mycosphaerella* and related anamorphs on banana. *Persoonia* 20: 19-37.
- Banke, S., Peschon, A. and McDonald, B.A. (2004). Phylogenetic analysis of globally distributed *Mycosphaerella graminicola* populations based on three DNA sequence loci. *Fungal Genetics and Biology* 41: 221-238.
- Barnes, I., Crous, P.W., Wingfield, B.D. and Wingfield, M.J. (2004). Multigene phylogenies reveal that red band needle blight of *Pinus* is caused by two distinct species of *Dothistroma*, *D. septosporum* and *D. pini*. *Studies in Mycology* 50: 551-565.
- Barr, M.E. (1972). Preliminary studies on the Dothideales in temperate North America. Contributions of the University of Michigan Herbarium 9: 523-638.
- Barr, M.E. (1996). *Planistromellaceae*, a new family in the Dothideales. *Mycotaxon* 60: 433-442.
- Batzer, J.C., Mercedes Diaz Arias, M., Harrington, T.C., Gleason, M.L., Groenewald, J.Z. and Crous, P.W. (2008). Four species of *Zygophiala* (*Schizothyriaceae*, *Capnodiales*) are associated with the sooty blotch and flyspeck complex on apple. *Mycologia* 100: 232-244.
- Beilharz, V. and Pascoe, I. (2002). Two additional species of *Verrucisporota*, one with a *Mycosphaerella* teleomorph, from Australia. *Mycotaxon* 82: 357-365.
- Braun, U. (1995). A *Monograph of Cercospora, Ramularia and Allied genera* (*Phytopathogenic Hyphomycetes*). Vol. 1. IHW-Verlag, Eching, Germany.
- Braun, U. (1998). A *Monograph of Cercospora, Ramularia and Allied genera* (*Phytopathogenic Hyphomycetes*). Vol. 2. IHW-Verlag, Eching, Germany.
- Braun, U. and Crous, P.W. (2006). (1732) Proposal to conserve the name *Pseudocercospora* against *Stigmia* and *Phaeoisariopsis* (*Hyphomycetes*). *Taxon* 55: 803.
- Braun, U. and Crous, P.W. (2007). The diversity of cercosporoid hyphomycetes – new species, combinations, names and nomenclatural clarifications. *Fungal Diversity* 26: 55-72.
- Braun, U., Crous, P.W., Dugan, F., Groenewald, J.G. and Hoog, S.G. de. (2003). Phylogeny and taxonomy of *Cladosporium*-like hyphomycetes, including *Davidiella* gen. nov., the teleomorph of *Cladosporium* s.str. *Mycological Progress* 2: 3-18.
- Braun, U., Crous, P.W. and Schubert, K. (2008). Taxonomic revision of the genus *Cladosporium* s. lat. 8. Reintroduction of *Graphiopsis* (= *Dichocladosporium*) with further reassessments of cladosporioid hyphomycetes. *Mycotaxon* 103: 207-216.
- Breejnen, A. den, Groenewald, J.Z., Verkley, G.J.M. and Crous, P.W. (2006). Morphological and molecular characterisation of *Mycosphaerella-ceae* associated with the invasive weed, *Chromolaena odorata*. *Fungal Diversity* 23: 89-110.
- Burgess, T.I., Barber, P.A., Sufaati, S., Xu, D., Hardy, G.E. StJ. and Dell, B. (2007). *Mycosphaerella* spp. on *Eucalyptus* in Asia; new species, new hosts and new records. *Fungal Diversity* 24: 135-157.
- Carlier, J., Foure, F., Gauhl, F., Jones, D.R., Lepoivre, P., Mourichon, X., Pasberg-Gauhl, C. and Romero, R.A. (2000). Black leaf streak. In: *Disease of Banana, Abaca and Enset* (ed. R.D. Jones). CABI Publishing, Wallingford, UK.: 37-47.
- Carnegie, A.J. and Keane, P.J. (1994). Further *Mycosphaerella* species associated with leaf diseases of *Eucalyptus*. *Mycological Research* 98: 413-418.
- Cheewangkoon, R., Crous, P.W., Hyde, K.D., Groenewald, J.Z. and To-anan, C. (2008). Species of *Mycosphaerella* and related anamorphs on *Eucalyptus* leaves from Thailand. *Persoonia* 21: 77-91.
- Chupp, C. (1954). A *Monograph of The Fungus Genus Cercospora*. Ithaca, New York. Published by the author.
- Conde-Ferrández, L., Waalwijk, C., Canto-Canché, B.B.,

- Kema, G.H.J., Crous, P.W., James, A.C. and Abeln, E.C.A. (2007). Isolation and characterization of the mating type locus of *Mycosphaerella fijiensis*, the causal agent of black leaf streak disease of banana. *Molecular Plant Pathology* 8: 111-120.
- Corlett, M. (1991). An annotated list of published names in *Mycosphaerella* and *Sphaerella*. *Mycologia Memoir* 18: 1-328.
- Cortinas, M.N., Crous, P.W., Wingfield, B.D. and Wingfield, M.J. (2006). Multi-gene phylogenies and phenotypic characters distinguish two species within the *Colletogloeopsis zuluensis* complex associated with *Eucalyptus* stem cankers. *Studies in Mycology* 55: 133-146.
- Crous, P.W. (1998). *Mycosphaerella* spp. and their anamorphs associated with leaf spot diseases of *Eucalyptus*. *Mycologia Memoir* 21: 1-170.
- Crous, P.W. and Alfenas, A.C. (1995). *Mycosphaerella gracilis* sp. nov. and other species of *Mycosphaerella* associated with leaf spots of *Eucalyptus* in Indonesia. *Mycologia* 87: 121-126.
- Crous, P.W. and Braun, U. (2003). *Mycosphaerella* and its anamorphs. 1. Names published in *Cercospora* and *Passalora*. *CBS Biodiversity Series* 1: 1-571.
- Crous, P.W. and Corlett, M. (1998). Reassessment of *Mycosphaerella* spp. and their anamorphs occurring on *Platanus*. *Canadian Journal of Botany* 76: 1523-1532.
- Crous, P.W. and Groenewald, J.Z. (2005). Hosts, species and genotypes: opinions versus data. *Australasian Plant Pathology* 34: 463-470.
- Crous, P.W. and Wingfield, M.J. (1996). Species of *Mycosphaerella* and their anamorphs associated with leaf blotch disease of *Eucalyptus* in South Africa. *Mycologia* 88: 441-458.
- Crous, P.W. and Wingfield, M.J. (1997). *Colletogloeopsis*, a new coelomycete genus to accommodate anamorphs of two species of *Mycosphaerella* occurring on *Eucalyptus*. *Canadian Journal of Botany* 75: 667-674.
- Crous, P.W., Aptroot, A., Kang, J.-C., Braun, U. and Wingfield, M.J. (2000). The genus *Mycosphaerella* and its anamorphs. *Studies in Mycology* 45: 107-121.
- Crous, P.W., Braun, U. and Groenewald, J.Z. (2007a). *Mycosphaerella* is polyphyletic. *Studies in Mycology* 58: 1-32.
- Crous, P.W., Braun, U., Schubert, K. and Groenewald, J.Z. (2007b). Delimiting *Cladosporium* from morphologically similar genera. *Studies in Mycology* 58: 33-56.
- Crous, P.W., Braun, U., Wingfield, M.J., Wood, A.R., Shin, H.-D., Summerell, B.A., Alfenas, A.C., Cumagun, C.J.R. and Groenewald, J.Z. (2009a). Phylogeny and taxonomy of obscure genera of microfungi. *Persoonia* 22: 139-161.
- Crous, P.W., Ferreira, F.A., Alfenas, A. and Wingfield, M.J. (1993a). *Mycosphaerella suberosa* associated with corky leaf spots on *Eucalyptus* in Brazil. *Mycologia* 85: 705-710.
- Crous, P.W., Ferreira, F.A. and Sutton, B.C. (1997). A comparison of the fungal genera *Phaeophleospora* and *Kirramyces* (coelomycetes). *South African Journal of Botany* 63: 111-115.
- Crous, P.W., Groenewald, J.Z. and Gams, W. (2003a). Eyespot of cereals revisited: ITS phylogeny reveals new species relationships. *European Journal of Plant Pathology* 109: 841-850.
- Crous, P.W., Groenewald, J.Z., Groenewald, M., Caldwell, P., Braun, U. and Harrington, T.C. (2006a). Species of *Cercospora* associated with grey leaf spot of maize. *Studies in Mycology* 55: 189-197.
- Crous, P.W., Groenewald, J.Z., Mansilla, J.P., Hunter, G.C. and Wingfield, M.J. (2004a). Phylogenetic reassessment of *Mycosphaerella* spp. and their anamorphs occurring on *Eucalyptus*. *Studies in Mycology* 50: 195-214.
- Crous, P.W., Groenewald, J.Z., Pongpanich, K., Himaman, W., Arzanlou, M. and Wingfield, M.J. (2004b). Cryptic speciation and host specificity among *Mycosphaerella* spp. occurring on Australian *Acacia* species grown as exotics in the tropics. *Studies in Mycology* 50: 457-469.
- Crous, P.W., Groenewald, J.Z., Summerell, B.A., Wingfield, B.D. and Wingfield, M.J. (2009b). Co-occurring species of *Teratosphaeria* on *Eucalyptus*. *Persoonia* 22: 38-48.
- Crous, P.W., Groenewald, J.Z., Wingfield, M.J. and Aptroot, A. (2003b). The value of ascospore septation in separating *Mycosphaerella* from *Sphaerulina* in the *Dothideales*: a Saccardoan myth? *Sydowia* 55: 136-152.
- Crous, P.W., Hong, L., Wingfield, M.J., Wingfield, B.D. and Kang, J.-C. (1999). *Uwebraunia* and *Dissoconium*, two morphologically similar anamorph genera with distinct teleomorph affinity. *Sydowia* 52: 155-166.
- Crous, P.W., Kang, J.-C. and Braun, U. (2001). A phylogenetic redefinition of anamorph genera in *Mycosphaerella* based on ITS rDNA sequence and morphology. *Mycologia* 93: 1081-1101.
- Crous, P.W., Liebenberg, M.M., Braun, U. and Groenewald, J.Z. (2006b). Re-evaluating the taxonomic status of *Phaeoisariopsis griseola*, the causal agent of angular leaf spot of bean. *Studies in Mycology* 55: 163-173.
- Crous, P.W., Schroers, H.-J., Groenewald, J.Z., Braun, U. and Schubert, K. (2006c). *Metulocladosporiella* gen. nov. for the causal organism of Cladosporium speckle disease of banana. *Mycological Research* 110: 264-275.
- Crous, P.W., Summerell, B.A., Carnegie, A.J., Mohammed, C., Himaman, W. and Groenewald, J.Z. (2007c). Follicolous *Mycosphaerella* spp. and their anamorphs on *Corymbia* and *Eucalyptus*. *Fungal Diversity* 26: 143-185.
- Crous, P.W., Summerell, B.A., Carnegie, A.J., Wingfield, M.J. and Groenewald, J.Z. (2009c). Novel species of *Mycosphaerellaceae* and *Teratosphaeriaceae*. *Persoonia* 23: In press.
- Crous, P.W., Summerell, B.A., Carnegie, A.J., Wingfield, M.J., Hunter, G.C., Burgess, T.I., Andjic, V.,

- Barber, P.A. and Groenewald, J.Z. (2009d). Unravelling *Mycosphaerella*: do you believe in genera? *Persoonia* 23: In press.
- Crous, P.W., Summerell, B.A., Mostert, L. and Groenewald, J.Z. (2008a). Host specificity and speciation of *Mycosphaerella* and *Teratosphaeria* species associated with leaf spots of *Proteaceae*. *Persoonia* 20: 59-86.
- Crous, P.W., Verkley, G.J.M. and Groenewald, J.Z. (2006d). *Eucalyptus* microfungi known from culture. 1. *Cladriella* and *Fulvoflamma* genera nova, with notes on some other poorly known taxa. *Studies in Mycology* 55: 53-63.
- Crous, P.W., Wingfield, M.J., Ferreira, F.A. and Alfenas, A. (1993b). *Mycosphaerella parkii* and *Phyllosticta eucalyptorum*, two new species from *Eucalyptus* leaves in Brazil. *Mycological Research* 97: 582-584.
- Crous, P.W., Wingfield, M.J. and Groenewald, J.Z. (2009e). Niche sharing reflects a poorly understood biodiversity phenomenon. *Persoonia* 22: 83-94.
- Crous, P.W., Wingfield, M.J., Mansilla, J.P., Alfenas, A.C. and Groenewald, J.Z. (2006e). Phylogenetic reassessment of *Mycosphaerella* spp. and their anamorphs occurring on *Eucalyptus*. II. *Studies in Mycology* 55: 99-131.
- Crous, P.W., Wingfield, M.J. and Park, R.F. (1991). *Mycosphaerella nubilosa* a synonym of *M. molleriana*. *Mycological Research* 95: 628-632.
- Crous, P.W., Wood, A.R., Okada, G. and Groenewald, J.Z. (2008b). Follicolous microfungi occurring on *Encephalartos*. *Persoonia* 21: 135-146.
- Debuchy, R. and Turgeon, B.G. (2006). Mating-type structure, evolution and function in euascomycetes. In: *The Mycota I. Growth, Differentiation and Sexuality* (eds. U. Kues and R. Fischer). Berlin, Germany: 293-323.
- Deighton, F.C. (1973). Studies on *Cercospora* and allied genera. IV. *Cercosporella* Sacc., *Pseudocercosporella* gen. nov. and *Pseudocercosporidium* gen. nov. *Mycological Papers* 133: 1-62.
- Deighton, F.C. (1976). Studies on *Cercospora* and allied genera. VI. *Pseudocercospora* Speg., *Pantospora* Cif. and *Cercoseptoria* Pter. *Mycological Papers* 140: 1-168.
- Deighton, F.C. (1979). Studies on *Cercospora* and allied genera. VII. New species and redispositions. *Mycological Papers* 144: 1-56.
- Deighton, F.C. (1987). New species of *Pseudocercospora* and *Mycovellosiella*, and new combinations into *Pseudocercospora* and *Phaeoramularia*. *Transactions of the British Mycological Society* 88: 365-391.
- Deighton, F.C. (1990). Observations on *Phaeoisariopsis*. *Mycological Research* 94: 1096-1102.
- Dugan, F.M., Braun, U., Groenewald, J.Z. and Crous, P.W. (2008). Morphological plasticity in *Cladosporium sphaerospermum*. *Persoonia* 21: 9-16.
- Essakhi, S., Mugnai, L., Crous, P.W., Groenewald, J.Z. and Surico, G. (2008). Molecular and phenotypic characterisation of novel *Phaeoacremonium* species isolated from esca diseased grapevines. *Persoonia* 21: 119-134.
- Farr, D.F., Bills, G.F., Chamuris, G.P. and Rossman, A.Y. (1995). *Fungi on Plants and Plant Products in The United States*. APS Press, St Paul, Minnesota, USA.
- Goodwin, S.B., Dunkle, D.L. and Zismann, V.L. (2001). Phylogenetic analysis of *Cercospora* and *Mycosphaerella* based on the internal transcribed spacer region of ribosomal DNA. *Phytopathology* 91: 648-658.
- Groenewald, M., Barnes, I., Bradshaw, R.E., Brown, A.V., Dale, A., Groenewald, J.Z., Lewis, K.J., Wingfield, B.D., Wingfield, M.J. and Crous, P.W. (2007). Characterization and distribution of mating type genes in the Dothistroma needle blight pathogens. *Phytopathology* 97: 825-834.
- Groenewald, M., Groenewald, J.Z., Braun, U. and Crous, P.W. (2006a). Host range of *Cercospora apii* and *C. beticola* and description of *C. apiicola*, a novel species from celery. *Mycologia* 98: 275-285.
- Groenewald, M., Groenewald, J.Z. and Crous, P.W. (2005). Distinct species exist within the *Cercospora apii* morphotype. *Phytopathology* 95: 951-959.
- Groenewald, M., Groenewald, J.Z., Harrington, T.C., Abeln, E.C.A. and Crous, P.W. (2006b). Mating type gene analysis in apparently asexual *Cercospora* species is suggestive of cryptic sex. *Fungal Genetics and Biology* 43: 813-825.
- Heitman, J. (2006). Sexual reproduction and the evolution of microbial pathogens. *Current Biology* 16: R711-R725.
- Heuchert, B., Braun, U. and Schubert, K. (2005). Morphotaxonomic revision of fungicolous *Cladosporium* species (hyphomycetes). *Schlechtendalia* 13: 1-78.
- Hoog, G.S. de, Hijwegen, T. and Batenburg-Van der Vegte, W.H. (1991). A new species of *Dissoconium*. *Mycological Research* 95: 679-682.
- Hunter, G.C., Crous, P.W., Carnegie, A.J. and Wingfield, M.J. (2009). *Teratosphaeria nubilosa*, a serious leaf disease pathogen of *Eucalyptus* spp. in native and introduced areas. *Molecular Plant Pathology* 10: 1-14.
- Hunter, G.C., Wingfield, B.D., Crous, P.W. and Wingfield, M.J. (2006). A multi-gene phylogeny for species of *Mycosphaerella* occurring on *Eucalyptus* leaves. *Studies in Mycology* 55: 147-161.
- Jackson, S.L., Maxwell, A., Neumeister-Kemp, H.G., Dell, B. and Hardy, G.E. StJ. (2004). Infection, hyperparasitism and conidiogenesis of *Mycosphaerella lateralis* on *Eucalyptus globulus* in Western Australia. *Australasian Plant Pathology* 33: 49-53.
- Kirschner, R. and Chen, C.J. (2007). Follicolous hyphomycetes from Taiwan. *Fungal Diversity* 26: 219-239.
- Klebahn, H. (1918). Haupt- und Nebenfruchtformen der Askomyzeten. Borntraeger Verlag, Leipzig, Germany.

- Laibach, F. (1922). Untersuchungen über einige *Ramularia*- und *Ovularia*-Arten und ihre Beziehungen zur Ascomycetengattung *Mycosphaerella* II. Zentralblatt für Bakteriologie Abt. II 55: 284-293.
- Lievens, B. and Thomma, B.P.H.J. (2005). Recent developments in pathogen detection arrays: implications for fungal plant pathogens and use in practice. *Phytopathology* 95: 1374-1380.
- Marin, D.H., Romero, R.A., Guzman, M. and Sutton, T.B. (2003). Black Sigatoka: an increasing threat to banana cultivation. *Plant Disease* 87: 208-222.
- Marincowitz, S., Groenewald, J.Z., Wingfield, M.J. and Crous, P.W. (2008). Species of Botryosphaeriaceae occurring on Proteaceae. *Persoonia* 21: 111-118.
- Maxwell, A., Jackson, S.L., Dell, B. and Hardy, G.E. StJ. (2005). PCR-identification of *Mycosphaerella* species associated with leaf diseases of *Eucalyptus*. *Mycological Research* 109: 992-1004.
- McDonald, B. and Linde, C. (2002). Pathogen Population genetics, evolutionary potential, and durable resistance. *Annual Review of Phytopathology* 40: 349-379.
- Merino, S.T., Nelson, M.A., Jacobson, D.J. and Natvig, D.O. (1996). Pseudohomothallism and evolution of the mating-type chromosome in *Neurospora tetrasperma*. *Genetics* 143: 789-799.
- Morris, M.J. and Crous, P.W. (1994). New and Interesting records of South African fungi. XIV. Cercosporoid fungi from weeds. *South African Journal of Botany* 60: 325-332.
- Müller, E. and Arx, J.A. von. (1962). Die Gattungen der Didymosporen Pyrenomyceten. *Beiträge zur Kryptogamenflora der Schweiz* 11: 1-922.
- Nag Raj, T.R. (1993). Coelomycetous anamorphs with appendage-bearing conidia. *Mycologue Publications*, Waterloo, Ontario, Canada.
- Nakashima, C., Motohashi, K., Meeboon, J. and To-anun, C. (2007). Studies on *Cercospora* and allied genera in northern Thailand. *Fungal Diversity* 26: 257-270.
- Nguyen, H.D.T. and Seifert, K.A. (2008). Description and DNA barcoding of three new species of *Leohumicola* from South Africa and the United States. *Persoonia* 21: 57-69.
- Park, R.F. and Keane, P.J. (1984). Further *Mycosphaerella* species causing leaf diseases of *Eucalyptus*. *Transactions of the British Mycological Society* 83: 93-105.
- Park, R.F., Keane, P.J., Wingfield, M.J. and Crous, P.W. (2000). Fungal diseases of eucalypt foliage. In: *Diseases and Pathogens of Eucalypts* (eds. P.J. Keane, G.A. Kile, F.D. Podger and B.N. Brown). CSIRO Publishing, Collingwood, Australia: 153-259.
- Pereira, O.L., Barreto, R.W., Cavallazzi, J.R.P. and Braun, U. (2007). The mycobiota of the cactus weed *Pereskia aculeata* in Brazil, with comments on the life-cycle of *Uromyces pereskiae*. *Fungal Diversity* 25: 127-140.
- Persoon, C.H. (1794). Nähere Bestimmung und Beschreibungen einiger sich nahe verwandter Pflanzen. *Annalen der Botanik* ed. Usteri 11: 1-32.
- Phillips, A.J.L., Alves, A., Pennycook, S.R., Johnston, P.R., Ramaley, A., Akulov, A. and Crous, P.W. (2008). Resolving the phylogenetic and taxonomic status of dark-spored teleomorph genera in the Botryosphaeriaceae. *Persoonia* 21: 29-55.
- Pretorius, M.C., Crous, P.W., Groenewald, J.Z. and Braun, U. (2003). Phylogeny of some cercosporoid fungi from *Citrus*. *Sydowia* 55: 286-305.
- Ramaley, A.W. (1991). *Clypeispora* and its *Mycosphaerella* teleomorph. *Mycotaxon* 40: 13-22.
- Ruibal, C., Platas, G., Bills, G.F. (2008). High diversity and morphological convergence among melanised fungi from rock formations in the Central Mountain System of Spain. *Persoonia* 21: 93-110.
- Schoch, C.L., Shoemaker, R.A., Seifert, K.A., Hambleton, S., Spatafora, J.W. and Crous, P.W. (2006). A multigene phylogeny of the Dothideomycetes using four nuclear loci. *Mycologia* 98: 1043-1054.
- Schubert, K., Braun, U., Groenewald, J.Z. and Crous, P.W. (2007a). Cladosporium leaf-blotch and stem rot of *Paeonia* spp. caused by *Dichocladosporium chlorocephalum* gen. nov. *Studies in Mycology* 58: 95-104.
- Schubert, K., Groenewald, J.Z., Braun, U., Dijksterhuis, J., Starink, M., Hill, C.F., Zalar, P., de Hoog, G.S. and Crous, P.W. (2007b). Biodiversity in the *Cladosporium herbarum* complex (*Davidiellaceae*, *Capnodiales*), with standardisation of methods for *Cladosporium* taxonomy and diagnostics. *Studies in Mycology* 58: 105-156.
- Scott, J.A., Untereiner, W.A., Ewaze, J.O., Wong, B. and Doyle, D. (2007). *Baudoinia*, a new genus to accommodate *Torula compniacensis*. *Mycologia* 99: 592-601.
- Shenoy, B.D., Jeewon, R. and Hyde, K.D. (2007). Impact of DNA sequence-data on the taxonomy of anamorphic fungi. *Fungal Diversity* 26: 1-54.
- Shin, H.D. and Kim, J.D. (2001). *Cercospora* and allied genera from Korea. *Plant Pathogens from Korea* 7: 1-302.
- Simon, U.K., Groenewald, J.Z. and Crous, P.W. (2009). *Cymadothea trifolii*, an obligate biotrophic leaf parasite of *Trifolium*, belongs to *Mycosphaerellaceae* as shown by nuclear ribosomal DNA analyses. *Persoonia* 22: 49-55.
- Stergiopoulos, I., Groenewald, M., Staats, M., Lindhout, P., Crous, P.W. and Wit, P.J.G.M. de. (2007). Mating-type genes and the genetic structure of a world-wide collection of the tomato pathogen *Cladosporium fulvum*. *Fungal Genetics and Biology* 44: 415-429.
- Stewart, E.L., Liu, Z., Crous, P.W. and Szabo, L. (1999). Phylogenetic relationships among some cercosporoid anamorphs of *Mycosphaerella* based on rDNA sequence analysis. *Mycological Research* 103: 1491-1499.

- Stukenbrock, E.H., Banke, S., Javan-Nikkhah, M. and McDonald, B.A. (2007). Origin and domestication of the fungal wheat pathogen *Mycosphaerella graminicola* via sympatric speciation. *Molecular Biology and Evolution* 24: 398-411.
- Summerell, B.A., Groenewald, J.Z., Carnegie, A.J., Summerbell, R.C. and Crous, P.W. (2006). *Eucalyptus* microfungi known from culture. 2. *Alysidiella*, *Fusculina* and *Phlogicylindrium* genera nova, with notes on some other poorly known taxa. *Fungal Diversity* 23: 323-350.
- Sutton, B.C. (1980). The coelomycetes. Fungi imperfecti with pycnidia, acervuli and stromata. Commonwealth Mycological Institute, Kew, UK.
- Sutton, B.C. and Crous, P.W. (1997). *Lecanostictopsis* gen. nov. and similar fungi from *Syzygium* species. *Mycological Research* 101: 215-225.
- Sutton, B.C. and Hennebert, G. (1994). Interconnections amongst anamorphs and their possible contribution to ascomycete systematics. In: *Ascomycete Systematics. Problems and Perspectives in The Nineties* (ed. D.L. Hawksworth), Nato ASI series 269. Plenum Press, New York, USA: 77-100.
- Sutton, B.C. and Waller, J.M. (1988). Taxonomy of *Ophiocladium hordei*, causing leaf lesions on *Triticale* and other *Gramineae*. *Transactions of the British Mycological Society* 90: 55-61.
- Swart, H.J. and Walker, J. (1988). Australian leaf-inhabiting fungi XXVIII. *Hendersonia* on *Eucalyptus*. *Transactions of the British Mycological Society* 90: 633-641.
- Taylor, J.E., Groenewald, J.Z. and Crous, P.W. (2003). A phylogenetic analysis of *Mycosphaerellaceae* leaf spot pathogens of *Proteaceae*. *Mycological Research* 107: 653-658.
- Tomilin, B.A. (1979). *Opredelitel' gribov roda Mycosphaerella* Johans. Nauka, Leningrad, USSR.
- Turgeon, B.G. (1998). Application of mating type gene technology to problems in fungal biology. *Annual Review of Phytopathology* 36: 115-137.
- Turgeon, B.G. and Yoder, O.C. (2000). Proposed nomenclature for mating type genes of filamentous ascomycetes. *Fungal Genetics and Biology* 31: 1-5.
- Verkley, G.J.M., Crous, P.W., Groenewald, J.Z., Braun, U. and Aptroot, A. (2004). *Mycosphaerella punctiformis* revisited: morphology, phylogeny, and epitypification of the type species of the genus *Mycosphaerella* (Dothideales, Ascomycota). *Mycological Research* 108: 1271-1282.
- Verkley, G.J.M. and Priest, M.J. (2000). *Septoria* and similar coelomycetous anamorphs in *Mycosphaerella*. *Studies in Mycology* 45: 123-128.
- Waalwijk, C., Heide, R. van der, Vries, I. de, Lee, T. van der, Schoen, C., Costrel-de Corainville, G., Hauser-Hahn, I., Kastelein, P., Kohl, J., Lonnet, P., Demarquet, T. and Kema, G.H.J. (2004). Quantitative detection of *Fusarium* species in wheat using TaqMan. *European Journal of Plant Pathology* 110: 481-494.
- Walker, J., Sutton, B.C. and Pascoe, I.G. (1992). *Phaeoseptoria eucalypti* and similar fungi on *Eucalyptus* with description of *Kirramyces* gen. nov. (Coelomycetes). *Mycological Research* 96: 911-924.
- Ware, S.B., Verstappen E.C.P., Breeden, J., Cavaletto, J.R., Goodwin, S.B., Waalwijk, C., Crous, P.W. and Kema, G.H.J. (2007). Discovery of a functional *Mycosphaerella* teleomorph in the presumed asexual barley pathogen *Septoria passerinii*. *Fungal Genetics and Biology* 44: 389-397.
- Zalar, P., Hoog, G.S. de, Schroers, H.-J., Crous, P.W., Groenewald, J.Z. and Gunde-Cimerman, N. (2007). Phylogeny and ecology of the ubiquitous saprobe *Cladosporium sphaerospermum*, with descriptions of seven new species from hypersaline environments. *Studies in Mycology* 58: 157-183.
- Zhan, J., Mundt, C.C. and McDonald, B.A. (2007). Sexual reproduction facilitates the adaptation of parasites to antagonistic host environments: Evidence from empirical study in the wheat-*Mycosphaerella graminicola* system. *International Journal for Parasitology* 37: 861-870.